New subgenus of leptarctine (Carnivora: Mustelidae) from the Late Miocene of Nebraska, U.S.A.

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Abstract.—A new subgenus, *Pseudoleptarctus,* is described on the basis of a mandible from the late Clarendonian (late Miocene). The new leptarctine differs from other species in having a rounded trigonid and a well-defined hypoconulid on m1 and an enlarged accessory cusp on p3. *Pseudoleptarctus genowaysi* has the largest dentition known for leptarctines. The morphological similarities to procyonids indicate their shared aspects of diet.

Mustelid carnivores occupy various habitats and their diet ranges from insects to vertebrates. Qiu & Schmidt-Kittler (1982) and Lim & Martin (2002) considered Leptarctinae to be a subfamily of mustelids including *Craterogale* (N. America, M. Miocene), *Trocharion* (Europe, M. Miocene), *Hypsoparia* (N. America, U. Miocene), and *Leptarctus* (N. America and Asia, L. to U. Miocene). *Leptarctus* is one of the least known fossil carnivores and it occurs in the middle and late Miocene of North America and the Miocene of the Tung Gur region, 13.5–13.8 MYA, Inner Mongolia, China (Lim 1997, Lim & Miao 2000, Lim et al. 2001, Lim & Martin 2002a, Zhai 1964). Leidy (1856) described a P4 from South Dakota (Fort Randall Formation, Barstovian) for *Leptarctus primus,* the type species. Wortman (1894) described a lower jaw with c1, p3, and p4 from Nebraska (Clarendonian) and referred the specimen to *L. primus.* However, Matthew (1924) erected a new species, *Leptarctus wortmani* Matthew, 1924 for the specimen (Runningwater Formation, E. Hemingfordian) previously described by Wortman (1894). Simpson (1930) described a P4 from Florida (Lower Bone Valley Formation, L. Barstovian-E. Clarendonian) as *Leptarctus progressus* and concluded that it shows some resemblance to *Nasua* in its greater width and larger protocone. Stock (1930) described a skull fragment with P4 and M1 from Oregon (Mascall Formation, E. Barstovian) as *L. oregonensis.* Olsen (1957) placed *Mephititaxus* (Thomas Farm Local Fauna, E. Hemingfordian) as *L. ancipidens.* In 1959, a skull, mandible, atlas, and axis were discovered from the Tung Gur region, Nei Mongol, China and described as *L. neimenguensis* (Zhai 1964). Lim & Miao (2000) described *L. martini* based on a well-preserved skull from Nebraska (Valentine Formation, L. Barstovian) and Lim & Martin (2001a) described *L. kansasensis* based on fragments of a skull fragment and maxillary bone with left P3 and P4 from Kansas (Blick Quarry, Clarendonian). Lim et al. (2001) described an incomplete skull with right M1 and left P4-M1 from Texas (Hemphill Beds, E. Hemphillian) for *L. supremus.* Lim & Martin (2001b) described an anterior portion of skull with left P2-M1 and right P3-M2 from Nebraska (Republican River Beds, E. Hemphillian) for *L. desuii.*

The mammalian diet is reflected in dental morphology, jaw shape, and masticatory muscles (Smith 1993). *Leptarctus* has dental characteristics indicative of diet different

from those of other mustelids. The upper incisors of *Leptarctus* can be distinguished by the peg-like and greatly reduced first and second upper incisors (Lim 1999b). The reduced upper canines suggest a non-carnivorous diet. The lower canine is strongly curved and grooved on its lingual side (Lim 1999a). A survey of the lower canines in modern carnivorous mammals revealed that the coati, *Nasua,* has a similar groove. *Nasua* is an omnivorous procyonid and one of the most frugivorous members of the Carnivora.

The edge of the masseteric fossa of the mandible is an insertion site for the masseter muscle which elevates and deviates the mandible while chewing (Turnbull 1970). The deep masseteric fossa of *Leptarctus* indicates a large masseter and suggests that *Leptarctus* could deviate the lower jaw laterally more than other mustelids. Olsen (1958) considered *L. ancipidens* to be a badger-like mustelid. However, the lower dentition of *L. ancipidens* (UF 5655) shows it differs more from *Taxidea taxus* than from *Procyon lotor*. The talonid on the m1 of *L. ancipidens* is long relative to the trigonid, a condition similar to the m1 of *Procyon lotor*. The talonid and trigonid of m1 in *Taxidea taxus* are of similar length. The m1 of *Pseudoleptarctus genowaysi* also has a long talonid (Fig. 1). This increased length of the talonid in *Leptarctus* and *Procyon* indicates that the anterior part of M1 that occluded with the talonid of m1 has increased its surface area. This structure shows that these animals had similar diets and needed a strong chewing capacity.

One distinction between *Leptarctus* and other mustelids is the great height of the zygomatic arches in *Leptarctus* (Lim 1996). The ventral edge of the zygomatic arch is an origin for the masseter, elevating the mandible and slightly deviating the mandible from side to side. The heavy zygomatic arch indicates a large masseter and suggests that *Leptarctus* had stronger chewing muscles than other mustelids.

Abbreviations used are: AMNH—De-partment of Vertebrate Paleontology, American Museum of Natural History; F:AM—Frick American Mammals, American Museum of Natural History; UF—Division of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, University of Florida; KUVP—Division of Vertebrate Paleontology, Natural History Museum and Biodiversity Research Center, University of Kansas; UNSM—Division of Vertebrate Paleontology, University of Nebraska State Museum.

Systematics

Order Carnivora Bowdich, 1821
Family Mustelidae Fischer von Waldheim, 1817
Subfamily Leptarctinae Gazin, 1936
Genus *Leptarctus* Leidy, 1856
Pseudoleptarctus, new subgenus

Diagnosis.—Large leptarctine with carnassial trigonid sub-equal in size to talonid and rounded anteriorly. The m1 crown is dominated by cross-lophs. The m2 is elongated. The p4 with primary and secondary cusps sub-equal in size. Thick cingula on premolars and molars.

Pseudoleptarctus genowaysi, new species
Figs. 1–3

Holotype.—UNSM 25470, a right mandible with p3-m1.

Type locality.—Cr-111, 2¼ mi SW of Burge P.O. on west side of the Snake River, Cherry County, Nebraska.

Referred specimens.—F:AM 25176, right mandible with canine, p3–4; F:AM 25211, left m1; F:AM 25167, right m1; F:AM 49412, left mandible with canine, p2-m2; F:AM 49413, right mandible with p3-m2.

Chronology.—Ash Hollow Formation, Late Clarendonian, Miocene.

Age.—*Pseudoleptarctus* refers to similarity to *Leptarctus. Pseudo* means false. The trivial name honors professor Hugh H. Genoways, former director of the University of
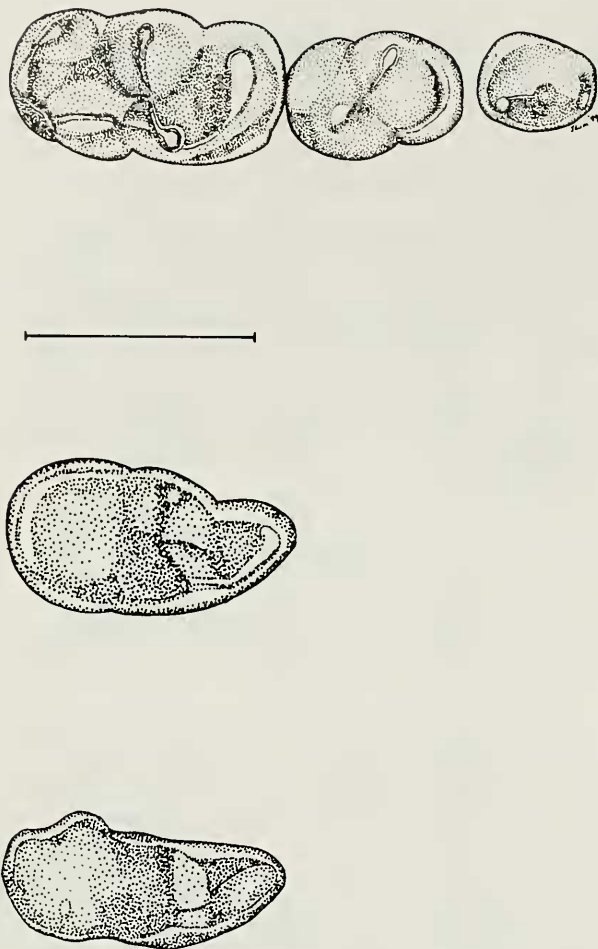
Fig. 1.   Occlusal view (right p3-m1) of *P. geno-waysi,* holotype, UNSM 25470, m1 of *L. wortmani* F:AM 25351 (middle) and m1 of *L. ancipidens* UF 5655 (bottom). Scale bar = 1 cm.

Nebraska State Museum, Lincoln, Nebraska.

Diagnosis.—Larger and more robust than *L. primus* and *L. wortmani.* The m1 has a labial cingulum, well-defined hypoconulid and the trigonid is rounded anteriorly. The m2 has a labial cingulum. Premolars and molar are more robust and rounded than in other *Leptarctus.* The second cusp of p4 enlarged and almost as big as the main cusp. The p3 has a small secondary cusp and a thick posterior cingulum.

Description.—The mandible is missing anterior parts of p3 and the ramus above the angular process. The dentition, p3–m1, is well-preserved. The teeth are more rounded and wider than in other *Leptarctus* (Fig. 1). The lower canines of F:AM 25176 and F:AM 49412 have a groove on the antero-labial side, characteristics of the leptarcti-

nes. The masseteric fossa is larger and deeper than in *L. primus* and *L. wortmani.*

In p3, a cingulum is located on the postero-lingual face of the tooth and a well-defined posterior accessory cusp is present postero-labially (Figs. 1–3).

The p4 has a round ridge on the anterior margin of the main cusp. The second cusp of p4 is well-developed and proportionately larger than in other *Leptarctus.*

The first molar has three large and high cusps on the trigonid. The metaconid is the highest cusp and a labial cingulum is present on the lateral surface of the connection between paraconid and protoconid. The talonid of m1 is expanded posteriorly by a median hypoconulid. The hypoconulid is connected to the hypoconid and the entoconid by a ridge. The second lower molar of F:AM 49412 has a labial cingulum, which differs from other species. The m2 is double-rooted and large and the mandibular foramen is deeper and more prominent compared to *L. primus* and *L. ancipidens.*

Discussion

The mandible (UNSM 25470) of *Pseudoleptarctus genowaysi* is the largest known leptarctine mandible. The presence of a distinctive cingulum in the labial side of m1 is unique among carnivores.

The lower canines of all leptarctines including *P. genowaysi* are curved and grooved on the lingual side. We know of no similar groove among modern carnivorous mammals with the exception of the coati, *Nasua* (Lim 1999a). *Nasua* is an omnivorous procyonid and one of the most frugivorous carnivores (Gompper & Decker 1998). The groove in both leptarctines and *Nasua* stops at the base of crown. *Solenodon,* a modern insectivore, has a deeper and broader groove on the antero-labial side of the lower canine as a conduit for toxic saliva, but the groove in *Solenodon* continues to the very edge of the lower jaw.

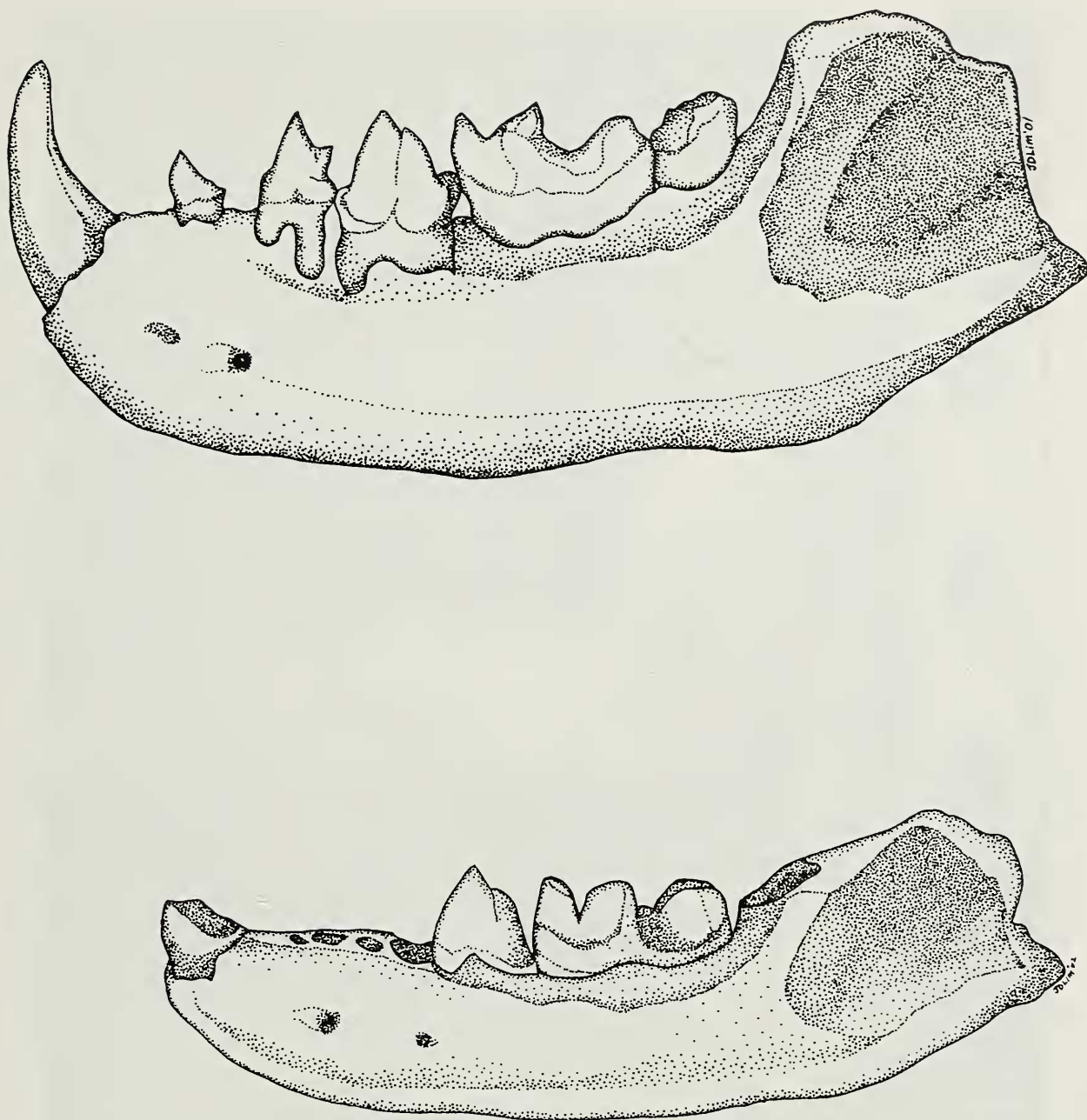The p3 and p4 of *P. genowaysi* are very similar to those of *Nasua nasua* in having

Fig. 2.   Lateral views of mandibles of *P. genowaysi* (F:AM 49412, above) and *L. primus* (AMNH 18270, bottom), ×1.5.

a postero-lingual cingulum. The presence of an accessory cusp on the postero-external face on p3 is similar to that in *L. wortmani* while other leptarctines do not have the accessory cusp. The dentition and mandible of *Pseudoleptarctus genowaysi* are robust and bigger than those of *L. wortmani* (Fig. 3). The height of mandible (below m1) of *P. genowaysi* (UNSM 25470) is 45% greater than in *L. wortmani* (F:AM 25351). The p4 shows some similarities to procyonids. The secondary cusp on p4 is well-defined and similar in size to the first cusp as in

Procyon lotor and *Nasua nasua*. Other leptarctines and living mustelids have a much smaller secondary cusp.

One of the most distinctive characters of the new species is the presence of a cingulum on the labial side of m1. The cingulum begins laterally at the paraconid and stops below the protoconid. The highest cusp of m1 is the metaconid while protoconids in *L. primus*, *L. wortmani*, and *L. ancipidens* are higher than the metaconid. The metaconids in *Procyon lotor* and *Nasua nasua* are also higher than the other

Fig. 3.   Mandibles of leptarctines in lateral view. a, *P. genowaysi* UNSM 25470, holotype; b, *L. primus* KUVP 9153; *L. ancipidens* UF 5655; d, *L. wortmani* cast of F:AM 25351. Scale bar = 5 cm.

Table 1.—Measurements (mm) of lower teeth and mandibles of *P. genowaysi, L. primus, L. wortmani* and *L. ancipidens*.

	P. genowaysi (UNSM 25470)	*L. primus* (AMNH 18270)	*L. wortmani* (F:AM 25351)	*L. ancipidens* (UF 5655)
Height of mandible (below m1)	14.5	8.5	10	15.7
p3: Length	5.2		5.5	4.9
Width	4.0		3.5	3
p4: Length	8.3	5.4	7.1	6.5
Width	5.1	3.3	4.1	4.1
m1: Length	11.7	9.6	11.1	10.7
Width	6.7	4.2	5.6	4.9
Length between p3–m1	26.1		23.4	22.7

cusps on m1. The width of m1 in *P. genowaysi* is 1.6 times wider than in *L. primus* (Table 1). The talonid of m1 in *P. genowaysi* is enlarged with well-defined cusps (hypoconid, hypoconulid, and entoconid) as in *Procyon lotor*.

The carnassial is a critical tooth in carnivorous mammals and major changes in its structure usually indicate changes in dietary preference. In general, the more carnivorous the diet the greater the emphasis on antero-posterior lophing of the trigonid coupled with reduction of the talonid. Herbivory is usually signaled by reduction of the trigonid and enlargement of the talonid. *Leptarctus* follows this pattern. Cross-lophing is also characteristic of the teeth of herbivorous mammals. *Pseudoleptarctus* presents an unusual mixture of these features. The trigonid is not reduced being about the same length as the talonid, but its anterior margin is squared so that the tooth pattern is dominated by cross-lophs. This creates a tooth even more modified towards herbivory than that of the raccoon, *Procyon lotor*, and in some ways similar to that of the leaf-eating koala bear, *Phascolarctos cinereus*. We have previously pointed out other similarities between *Leptarctus* and koalas, and think that leaf-eating might have played a role in the leptarctine diet, especially in *Pseudoleptarctus* (Lim 1997, 1999). Examination of the muscle insertions indicates a greater capacity to deviate the mandible when chewing and this probably contributes to the rearrangement of cusps and the

accentuation of cross-lophs. The lack of trigonid reduction (already present in *Leptarctus*) and the large double rooted m2 (as shown by the alveoli) are primitive character states as compared to *Leptarctus* and show that *Pseudoleptarctus* is not simply a late occurring and advanced species of *Leptarctus* but a separate line that split off early in leptarctine evolution. The widening of the trigonid occurs in parallel with widening of the p4 through enlargement of the secondary cusp and accentuation of the cingulum. Chewing force has shifted forward and this is reflected in a slight forward extension of the masseteric fossa as compared to *Leptarctus*. The reduced peg-like central incisors and the outward divergence of the canines in leptarctines suggests some specialized function and might have provided an exit for a long, slender, mobile tongue.

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